

SOCIAL ORGANIZATION IN *LEPTOTHORAX* ANTS: WITHIN- AND BETWEEN-SPECIES PATTERNS*

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Recent application of quantitative techniques to behavior (cf. Colgan 1978) has resulted in new approaches to understanding social interactions among animals. A technique particularly widely-used for study of ant colonies is development of the colony ethogram, or behavioral profile. We now have ethogram information for a wide variety of species. Most reports in the literature focus on a single colony (Table 1); variation within a species is rarely discussed. In addition, the colony time budget, an important second class of information, is generally not reported (Table 1). The appropriateness of behavioral comparisons across species is thereby severely limited by availability of only one type of behavior frequency catalog, for only one colony per species.

Caste complexity and division of labor related to morphological or age variation comprise another type of information contributing to an understanding of social organization. As a rule, queens have smaller repertoires than do workers; majors have different ethograms than minors; and older workers display different behavior frequencies than do younger workers. Studies of morphology affecting behavior have concentrated on polymorphic species for which discrete worker castes can be distinguished; recent work has shown that, even for monomorphic species, worker size can bias behavior (Wilson 1978, Herbers and Cunningham 1983).

A reasonably complete description of social organization for an ant species should treat ethograms, time budgets, and behavioral caste specialization, both within and between different colonies. Here I report such details for three colonies of *Leptothorax ambiguus*. This information is then compared to data from the closely-related *L. longispinosus* to arrive at an understanding of between- and within- species variation in social behavior.

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Table 1. Ethograms for many ant species have been published, but variation between colonies is rarely reported.

Species	# of Colonies Observed	# of Colony Ethograms Reported	Time Budget Reported?	Reference
<i>Amblyopone pallipes</i>	5	1	no	Traniello 1982
<i>Atta sexdens</i>	1	1	no	Wilson 1980
<i>Campanotus (Colobopsis) sp.</i>	1	1	no	Cole 1980
<i>Cephalotes atratus</i>	1	1	yes	Corn 1980
<i>Formica perpilosa</i>	1	1	no	Brandao 1978
<i>Leptothorax curvispinosus</i>	2	1	no	Wilson & Fagen 1974
<i>Leptothorax longispinosus</i>	4	4	no	Herbers 1982
<i>Leptothorax longispinosus</i>	4	1	yes	Herbers & Cunningham 1983
<i>Orectognathus versicolor</i>	1	1	no	Carlin 1982
<i>Pheidole dentata</i>	1	1	no	Wilson 1976a
<i>Solenopsis geminata</i>	1	1	no	Wilson 1978
<i>Solenopsis invicta</i>	1	1	no	Wilson 1978
<i>Zacryptocerus varians</i>	2	1	no	Wilson 1976b
<i>Zacryptocerus varians</i>	1	1	no	Cole 1980

METHODS

Colonies of *L. ambiguus* were collected in May 1982 from the E. N. Huyck Preserve (Albany County, NY). These colonies were settled in artificial nest boxes and maintained according to standard methods (Herbers and Cunningham 1983); in addition, frozen fruit-flies were provided as a food source.

For detailed observations, three colonies were chosen on the basis of queen and worker number to match earlier studies of *L. longispinosus* (Herbers 1982). All *Leptothorax* colonies studied were of approximately equal worker number, all had eggs and larvae, and all produced alates by summer's end; only queen number varied significantly (Table 2).

Behavioral observations were conducted June 9—August 24, 1982 through a Wild M5-A stereomicroscope as follows: a worker was chosen at random and all her actions were recorded over a 30-minute period. In addition, activities of individuals around her in the field of view were recorded. Head widths of the randomly-chosen ants were measured at a standard depth of field, by use of an ocular micrometer.

Data analysis followed methods outlined by Fagen and Goldman (1977) for behavior catalogs; Herbers and Cunningham (1983) for statistical evidence of polyethism and morphological bias; and Cole (1980) for producing dendrograms.

Table 2. Colony sizes of *Leptothorax* used in this comparative study. Data on *L. longispinosus* were reported by Herbers (1982).

	Original # of Queens	Original # of Workers	Eggs Laid?	Larvae Present?	Alates Reared?
<i>Leptothorax ambiguus</i>					
La-A	3	27	yes	yes	yes
La-B	1	28	yes	yes	yes
La-C	0	20	yes	yes	yes
<i>Leptothorax longispinosus</i>					
L1-A	1	30	yes	yes	yes
L1-B	1	31	yes	yes	yes
L1-C	5	28	yes	yes	yes
L1-D	4	36	yes	yes	yes

RESULTS AND DISCUSSION

Social Organization of L. ambiguus colonies

A total of 60 hours were recorded over the three colonies for a grand total of 3145 observations. Ethograms for the three colonies of *L. ambiguus* are reported in Table 3. A total of 46 behaviors were recorded for workers and 13 for queens. Despite the large catalog size, no behavior was unique to *L. ambiguus*; all in Table 3 are relatively common to many species included in Table 1.

As expected, queens were much less active than workers (Table 3). Their behavior was almost exclusively directed towards the brood; the exceptional occasion for colony La-B occurred when a queen was observed walking outside the nest and taking a drink; she later returned inside. Because of the paucity of data on queen behavior, analyses below concern only worker behavior.

Frequencies of observations for behaviors over three colonies are given in Figure 1. Sample coverages were uniformly greater than 99% (Figure 1). Consequently inferences about the true colony repertoire can safely be made. There was considerable variation among colonies (Figure 1), yet the distributions were not significantly different from each other ($\chi^2 = 13.80$, 14 df, $P > .05$). Thus distributions of observations over all behavior categories were roughly equivalent.

Comparisons of absolute frequencies among colonies showed that many worker behaviors were observed in all colonies (Table 3). For some, ethogram frequencies were nearly equal (IL, CP, ATW, RW) whereas for others the correspondences were not good (RE, IE, ALW). A third class of behaviors included those observed for only one or two nests (CE, FLD, AAE, CR). Thus considerable inter-nest variation existed. For a given colony, some behaviors known to occur in the species were missing from the ethogram, some were common or rare relative to other colonies, and some were equally frequent to others. Despite apparent discrepancies in absolute frequencies, the rankings of behaviors by frequency were similar over the three colonies (Kendall's coefficient of concordance; $W = .864$, 27 df, $P < .001$). That is, behaviors commonly observed in one colony were also common in others whereas those rare in one tended to be rare in all. In particular, behaviors missing from one colony's ethogram were generally rare in others. Therefore, although absolute frequency varied from nest to nest, relative frequencies were similar.

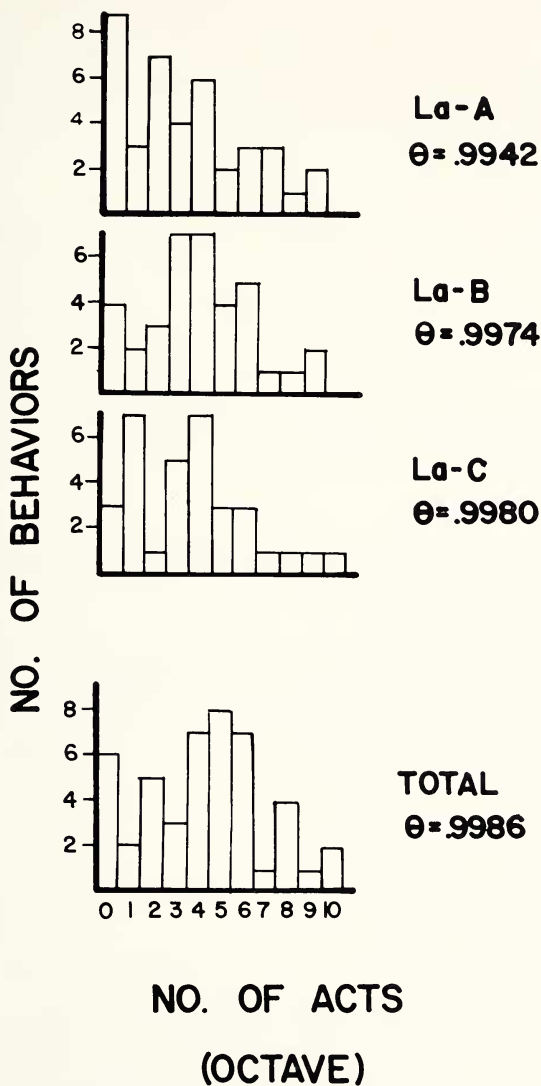


Figure 1. Abundance histograms for three colonies of *L. ambiguus* and for pooled data. The abscissa gives the number of observations per behavior, to the base 2; thus octave 0 indicates behaviors observed once, octave 1 refers to exactly 2 observations, octave 2: 3 or 4 observations, octave 3: 5 through 8, and so on. The largest octave, 10 refers to behaviors observed 513–1024 times. The value of θ given for each data set indicates the sample coverage, as described by Fagen and Goldman (1977).

Table 3. Ethograms for three colonies of *L. ambiguus*. Since Colony La-C was queenless, no data on queen behavior are reported.

Code Behavior	Workers			Queens	
	La-A (N=1145)	La-B (N=1169)	La-C (N=831)	La-A (N=18)	La-B (N=14)
Personal Behavior					
RE Rest	.1519	.1104	.2078	—	—
SG Self-Groom	.2155	.2211	.1378	.17	.21
MO Move inside Nest	.2892	.3298	.3584	—	—
Brood Care					
IE Inspect Egg	.0026	.0123	.0088	.22	.07
GE Groom Egg	.0006	.0058	.0061	.06	—
CE Carry Egg	—	.0032	.0061	.11	.07
LE Lay Egg	—	—	—	.11	.14
AL Assist Egg-Laying	—	—	—	—	.07
IL Inspect Larva	.0415	.0336	.0292	.17	—
GL Groom Larva	.0461	.0336	.0428	.06	—
CL Carry Larva	.0058	.0071	.0149	—	—
RL Regurgitate w/Larva	.0084	.0052	.0061	—	—
FLD Feed Larva Solid	—	—	.0014	—	—
ALE Assist Larval Ecdysis	.0026	.0006	—	—	—
IP Inspect Pupa	.0019	.0052	.0102	—	—
GP Groom Pupa	.0039	.0039	.0061	.05	.21
CP Carry Pupa	.0006	.0006	.0014	—	.14
AAE Assist Adult Eclosion	—	.0019	—	—	—
Social Interactions					
BC Be Carried	—	—	.0007	—	—
ATW Antennate Worker	.0454	.0472	.0570	—	—
ATB Antennate Body	.0058	.0084	.0061	—	—

RW Regurgitate w/ Worker	.0441	.0271	.0380	—
ALW Allogroom Worker	.0195	.0310	.0156	—
BG Be Groomed	.0019	.0142	.0048	—
ATQ Antennate Queen	.0006	.0026	—	—
ALQ Allogroom Queen	—	.0006	—	—
RQ Regurgitate w/ Queen	.0013	.0013	—	—
FQ Fight Queen	—	—	—	.06
Social Interactions (continued)				
ATM Antennate male	.0006	—	—	—
ALM Allogroom Male	.0026	—	—	—
CM Carry Male	.0013	—	—	—
RM Regurgitate w/ Male	.0006	—	—	—
ALF Allogroom Alate Female	—	—	.0007	—
Physical Nest Maintenance				
LN Lick Nest Wall	.0039	.0065	.0129	—
LOT Look Outside Nest	.0091	.0271	.0027	—
LEx Inspect Exuvium	.0006	.0013	—	—
CEX Carry Exuvium	.0006	.0045	.0034	—
EEX Eat Exuvium	.0006	.0058	.0041	—
HM Handle Nest Material	.0019	.0110	.0041	—
CR Carry Refuse	.0006	—	—	—
Provisioning				
FF Forage	.0221	.0058	.0014	—
MOT Move Outside	.0195	—	.0014	.07
IDr Inspect Prey	.0052	.0039	.0007	—
CDr Carry Prey	.0019	.0026	.0014	—
EDr Eat Prey	.0071	—	—	—
FdN Feed Inside Nest	.0013	.0065	.0054	—
FDO Feed Outside Nest	.0058	.0006	.0014	—
IFd Inspect Food	.0032	—	—	—
DR Drink	.0214	.0045	.0014	.07

Table 3. Ethograms for three colonies of *L. ambiguus*. Since Colony La-C was queenless, no data on queen behavior are reported

Code	Behavior	Workers			Queens	
		La-A (N=1145)	La-B (N=1169)	La-C (N=831)	La-A (N=18)	La-B (N=14)
Personal Behavior						
RE	Rest	.1519	.1104	.2078	—	—
SG	Self-Groom	.2155	.2211	.1378	.17	.21
MO	Move inside Nest	.2892	.3298	.3584	—	—
Brood Care						
IE	Inspect Egg	.0026	.0123	.0088	.22	.07
GE	Groom Egg	.0006	.0058	.0061	.06	—
CE	Carry Egg	—	.0032	.0061	.11	.07
LE	Lay Egg	—	—	—	.11	.14
AL	Assist Egg-Laying	—	—	—	—	.07
IL	Inspect Larva	.0415	.0336	.0292	.17	—
GL	Groom Larva	.0461	.0336	.0428	.06	—
CL	Carry Larva	.0058	.0071	.0149	—	—
RL	Regurgitate w/Larva	.0084	.0052	.0061	—	—
ELD	Feed Larva Solid	—	—	.0014	—	—
ALE	Assist Larval Ecdysis	.0026	.0006	—	—	—
IP	Inspect Pupa	.0019	.0052	.0102	—	—
GP	Groom Pupa	.0039	.0039	.0061	.05	.21
CP	Carry Pupa	.0006	.0006	.0014	—	.14
AAE	Assist Adult Ecdision	—	.0019	—	—	—
Social Interactions						
BC	Be Carried	—	—	.0007	—	—
ATW	Antennate Worker	.0454	.0472	.0570	—	—
ATB	Antennate Body	.0058	.0084	.0061	—	—
RW	Regurgitate w/Worker	.0441	.0271	.0380	—	—
ALW	Allogroom Worker	.0195	.0310	.0156	—	—
BG	Be Groomed	.0019	.0142	.0048	—	—
ATQ	Antennate Queen	.0006	.0026	—	—	—
ALQ	Allogroom Queen	—	.0006	—	—	—
RQ	Regurgitate w/Queen	.0013	.0013	—	—	—
FQ	Fight Queen	—	—	—	.06	—
Social Interactions (continued)						
ATM	Antennate male	.0006	—	—	—	—
ALM	Allogroom Male	.0026	—	—	—	—
CM	Carry Male	.0013	—	—	—	—
RM	Regurgitate w/Male	.0006	—	—	—	—
ALF	Allogroom Alate Female	—	—	.0007	—	—
Physical Nest Maintenance						
LN	Lick Nest Wall	.0039	.0065	.0129	—	—
LOT	Look Outside Nest	.0091	.0271	.0027	—	—
LEx	Inspect Exuvium	.0006	.0013	—	—	—
CEx	Carry Exuvium	.0006	.0045	.0034	—	—
EEx	Eat Exuvium	.0006	.0058	.0041	—	—
HM	Handle Nest Material	.0019	.0110	.0041	—	—
CR	Carry Refuse	.0006	—	—	—	—
Provisioning						
FF	Eorage	.0221	.0058	.0014	—	—
MOT	Move Outside	.0195	—	.0014	—	—
IDr	Inspect Prey	.0052	.0039	.0007	—	.07
CDr	Carry Prey	.0019	.0026	.0014	—	—
EDr	Eat Prey	.0071	—	—	—	—
FdN	Feed Inside Nest	.0013	.0065	.0054	—	—
FDO	Feed Outside Nest	.0058	.0006	.0014	—	—
IFd	Inspect Food	.0032	—	—	—	—
DR	Drink	.0214	.0045	.0014	—	.07

Table 4. Time budgets for *L. ambiguus* workers.

Behavior	Proportion of Time (p_t)			
	La-A	La-B	La-C	Total
RE	.6362	.5985	.8157	.68064
SG	.0565	.0922	.0153	.05520
MO	.1453	.1384	.1281	.13753
IE	.0016	.0056	—	.00242
GE	.0003	.0018	—	.00072
CE	—	.0013	—	.00044
IL	.0144	.0117	.0051	.01052
GL	.0282	.0115	.0034	.01478
CL	.0022	—	—	.00078
RL	.0077	.0018	—	.00331
FLD	—	—	—	—
ALE	—	.0012	—	.00040
IP	.0007	.0018	.0024	.00158
GP	.0017	.0030	.0012	.00196
CP	—	—	—	—
AAE	.0008	.0009	—	.00029
ATW	.0048	.0070	.0066	.00611
ATB	.0011	.0013	.0015	.00129
RW	.0235	.0167	.0103	.01704
ALW	.0039	.0153	.0005	.00658
BG	.0055	.0449	.0058	.01864
ATQ	—	.0001	—	.00002
ALQ	—	—	—	—
RQ	—	—	—	—
ATM	—	—	—	—
ALM	—	—	—	—
CM	—	—	—	—
RM	—	—	—	—
ALF	—	—	—	—
BC	—	—	—	—
LN	.0028	.0024	.0002	.00184
LOT	.0013	.0100	.0001	.00378
IE _x	.0001	.0008	—	.00032
CE _x	—	.0024	.0012	.00119
EE _x	—	.0020	.0014	.00111
HM	—	.0020	.0007	.00089
CR	—	—	—	—
FF	.0010	—	—	.00036
MOT	.0293	.0120	—	.01424
ID _r	.0001	.0030	.0001	.00107

Table 4. Time budgets for *L. ambiguus* workers. (Continued)

Behavior	Proportion of Time (p_t)			Total
	La-A	La-B	La-C	
CDr	—	.0042	—	.00139
EDr	.0291	—	—	.01021
FdN	—	.0065	.0004	.00229
FdO	.0005	—	—	.00016
IFd	.0005	—	—	.00017
DR	.0008	—	—	.00027

Time budgets for workers of the three colonies are given in Table 4. The largest elements in Table 4 correspond to resting; overall, workers spent 68% of the time motionless. It is interesting to note that the most sedentary colony was La-C, which had no queen; perhaps the high rate of inactivity was related to a lower rate of egg production or overall lack of queen stimulation. Even so, resting was predominant for all nests. The second dominant behavior was moving inside the nest, on average accounting for 13.8% of the worker time budget. In addition, self grooming was a large contributor in all colonies observed, consuming on average 5% of worker's time. Thus personal behavior accounted for the vast majority of the time budget; activities which can be called "social" consumed less than 15% of the workers' time.

Among social behaviors, time budget variation among colonies was minimal for some types (GP, ATW, ATB). Proportions of time spent in other behaviors were quite different among colonies; the most extreme case was LOT, which varied by two orders of magnitude ($p_t = .0100$ for La-B and $.0001$ for La-C). Kendall's test for concordance showed that, despite differences in absolute proportion of time, rankings of behaviors by relative proportions were similar over all colonies ($W = 0.763$, 13 df, $P < .005$). That is, behaviors consuming a large portion of the time budget in one colony tended to be important for other colonies, and behaviors rare in one colony were usually rare in all. Despite quantitative differences in specific types of activity, overall qualitative agreement in time budgets was strong.

To sum, no significant differences in relative importance of behaviors were observed over the three colonies. Histograms of behavior frequency (Fig. 1), rankings of ethogram frequency (Table 3) and relative time budget frequencies (Table 4) were not significantly different. Therefore, in subsequent analyses of within-species social organization below, data were pooled over three colonies. I will return to consideration of between-colony variation below.

Division of labor among workers was investigated by considering the matrix of transition frequencies among behaviors listed in the ethogram. Within this 46 x 46 matrix, elements indicate how often each behavior followed and preceded every other behavior. To simplify presentation of the results, transitions among behaviors listed in the ethogram are synopsized in Table 5. Diagonal elements represent the frequencies by which behaviors in the same categories followed each other whereas off-diagonal elements represent transition frequencies between behaviors in different groups (Herbers and Cunningham 1983). Division of labor is implicated if nonzero transition frequencies are clustered in diagonal blocks of the matrix and zeroes occur in off-diagonal blocks.

Examination of Table 5 shows that transitions from (column 1) and into (row 1) Personal Behavior commonly occurred. This is no surprise, since virtually all workers displayed a form of personal behavior. However, among social behaviors, the overall distribution of nonzero transitions deviated strongly from random expectation ($G = 55.24$, 16 df, $P < .001$), in a pattern consistent with organization of behaviors into roles: behaviors within the group Brood Care were positively correlated in time, as were those within the groups Social Interactions, Physical Maintenance, and Colony Provisioning. Between these groups, there were significantly fewer transitions than random expectation (Table 5). The pattern of overabundance of nonzero transitions in diagonal blocks, and under-representation in off-diagonal blocks was absolutely consistent with expectation. Overall, nonzero transitions clustered in diagonal blocks, thereby providing statistical evidence of polyethism.

Worker behavior can be provisionally categorized into four roles: brood care, social interactions, physical nest maintenance, and provisioning, since transitions among behaviors within a role occurred more often than random expectation whereas links between roles occurred less often than by chance. Information from the single-step

Table 5. Synopsis of one-step transition probabilities among worker behaviors. Entries indicate the number of nonzero transitions from Behavior i to Behavior j observed over three colonies.

Behavior i	Behavior j				
	Personal Behavior	Brood Care	Social Interactions	Physical Maintenance	Provisioning
Personal Behavior	9	20	15	8	9
Brood Care	16	33 ⁺	6 ⁻	2 ⁻	0 ⁻
Social Interactions	14	8	17 ⁺	0 ⁻	2 ⁻
Physical Maintenance	7	2 ⁻	1 ⁻	7 ⁺	1 ⁻
Provisioning	8	0 ⁻	2 ⁻	3 ⁻	21 ⁺

⁺ more than expected by chance

⁻ fewer than expected by chance

G = 55.24, 16 df, P < .001

transition matrix therefore gave important insights to the nature of polyethism in *L. ambiguus*. However, Table 5 must be interpreted with caution, since it does not report linkage over several acts. Analysis of per-second transition probabilities cannot detect transitions between behaviors intervened by other acts. That is, over a relatively long period, workers may switch roles, which would not be disclosed by single-step transition analysis (Herbers and Cunningham 1983). While single-step transitions suggest patterns of polyethism, inferences must be corroborated by long-term observations of behavior.

Information on worker behavior over 30-minute periods is given in Table 6. There is indicated the number of ants (out of a total of 57) that executed two behaviors within a 30-minute period. It is clear from Table 6 that behaviors provisionally assigned to different roles were often displayed by one worker over 30-minutes' time. Results of statistical testing of Table 6 are summarized by Venn diagrams in Figure 2. Behaviors intersecting in this figure co-occurred more often than expected by chance (χ^2 tests) whereas sets not intersecting were observed for the same individuals at a rate no different from chance expectation. Thus behaviors involved in egg care were related, as were those concerning care of larvae and those related to

care of pupae. However, no greater proportion of egg-workers also tended for larvae and pupae than chance expectation. That is, individuals specializing on eggs were not necessarily those specializing on pupae or larvae. The final set of behaviors is a large but loosely-connected cluster. Regurgitation, grooming, and antennation were closely interconnected (Figure 2); these were also peripherally connected with inspecting the nest exterior and moving outside, since individuals returning from an outside foray elicited interest and grooming from nestmates. Similarly, LN and HM do not directly intersect, since they co-occurred no more often than chance expectation; these two behaviors were indirectly linked through ATW and RW (Figure 2). Behaviors in the roles of social interactions, physical maintenance, and provisioning were therefore not strongly separated.

Thus analysis of sets of behaviors displayed over 30-minute periods illustrated the expectation that individual workers tended to specialize, particularly within the brood care role. An ant grooming larvae was more likely to also carry or regurgitate to larvae than chance expectation. By a similar token, a worker guarding the nest

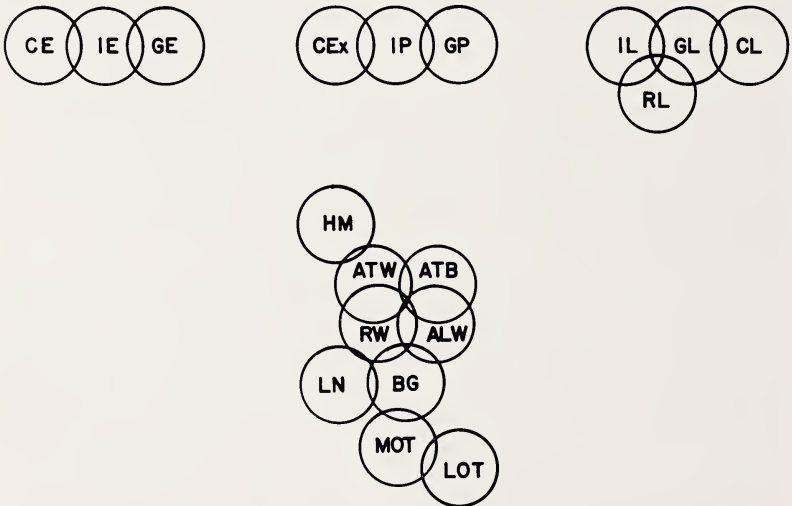


Figure 2. Sets of behaviors that co-occurred within 30-minutes. Two intersecting behaviors were observed more often than expected by chance (χ^2 tests; for all intersections $P < .05$). Behaviors not intersecting occurred as often or less than random expectation.

entrance (LOT) was likely to move outside the nest, then to be groomed by nestmates upon reentry. Thus some components of polyethism were statistically verified by examination of long-term individual worker behavior. However, the division of labor inferred from Table 6 was considerably weaker than the instantaneous transition matrix (Table 5) suggested. Individuals involved in brood care acts also displayed behaviors in other roles over a 30-min. period. Likewise, co-occurrences of behaviors in other roles were very common. The pattern emerging from consideration of all data is that workers strongly specialized in the short-term but over 30-minutes the specialization was weakened.

A final component of social organization is morphological bias in polyethism. Worker size is known to be correlated with behavior in many species, including the monomorphic *L. longispinosus* (Herbers and Cunningham 1983). The range of worker sizes in *L. ambiguus* is indicated in Figure 3. Pooled data are drawn there, since

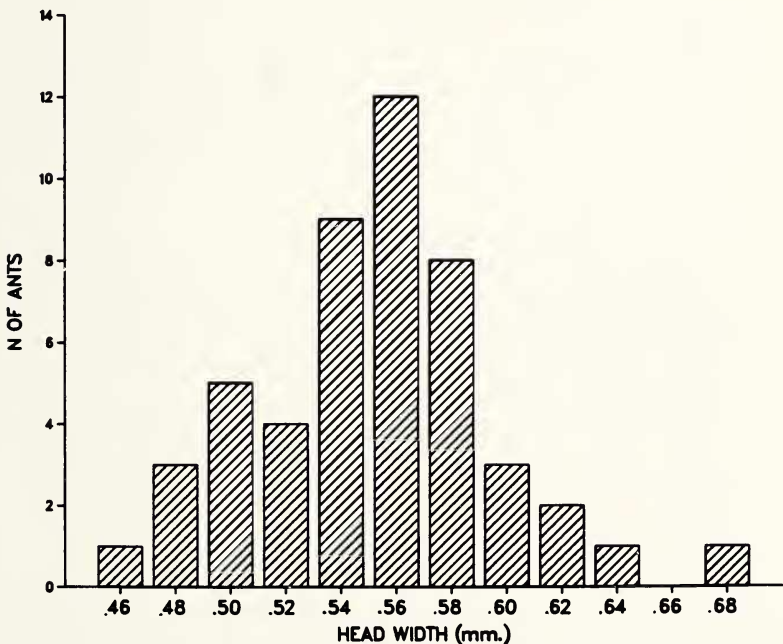


Figure 3. Morphological variation in *L. ambiguus* workers. Head width distribution was normal, and the largest worker was less than 1.5 times that of the smallest.

distributions were not significantly different among colonies (ANOVA, $F = .09$, 2 df, $P < .05$). Head widths were relatively invariant in this species ($\bar{x} = .552$ mm, $s = .043$ mm) such that the largest individual was less than 1.5 \times the smallest (Figure 3). Thus the potential for size-biased polyethism was quite restricted.

Head widths of workers displaying different ethogram behaviors were considered. Data were again pooled over three colonies since mean head widths did not differ significantly for any behavior (ANOVA with variable df; in all cases $P < .05$). Figure 4 illustrates statistics of head width for workers displaying each behavior. No obvious differentiation of head width according to roles can be discerned. Analysis of data in Figure 4 is summarized in Table 7, which is based on ANOVA's for differences between mean head widths (LSD tests). Most of the significant differences separate workers regurgitating with larvae from other behaviors (row and column headed RL in Table 7). That workers displaying RL were on average larger than others is evident from Figure 4. Starred entries of Table 7 are sporadic; certainly patterns of differences in mean head width showed no clear segregation by roles. Workers exhibiting a brood care behavior were not more similar in size to those displaying other brood care behaviors than they were to workers involved in social interactions or provisioning. Thus there was no apparent morphological bias underlying polyethism for *L. ambiguus*.

The overall picture that emerges of *L. ambiguus* social organization is short-term specialization of individual on task according to four roles: brood care, social interactions, physical nest maintenance, and provisioning (Table 3). However, the division of labor was rather loose, since switching between roles was often observed over 30-minute periods (Table 4). The nonrandom co-occurrence of sets of behaviors (Figure 2) statistically reinforced inferences about polyethism from the transition matrix. Finally, no strong morphological bias was demonstrated for ants specializing on specific tasks.

Comparison with L. longispinosus

Results of this study were compared with data from its closely-related congener *L. longispinosus*; such comparisons were valid since all observations were conducted in the same laboratory using standard husbandry techniques. The major difference in culture conditions between species was the addition of fruitflies to *L. ambiguus* diets. The earlier study had not incorporated feeding insect prey

Table 6 (continued).

	IP	GP	AAE	ATW	ATB	RW	ALW	BG	ATQ	LN	LOT	
56	RG											
45	SG											
51	MO											
6	IE											
4	GE											
1	CE											
21	IL											
16	GL											
2	CL											
4	RL											
1	ALE											
10	IP	—										
5	GP	5	—									
1	AAE	1	0	—								
36	ATW	7	2	1	—							
14	ATB	2	1	0	13	—						
25	RW	4	1	1	21	11	—					
7	ALW	1	1	0	7	5	6	—				
15	BG	2	1	0	13	5	10	5	—			
1	ATQ	0	1	0	1	0	0	0	0	—		
9	LN	0	0	0	8	3	7	2	6	0	—	
8	LOT	0	0	0	7	2	5	2	4	0	2	—
2	IE _x	1	0	1	2	0	2	0	0	0	0	0
3	CE _x	2	0	1	3	1	2	0	1	0	0	0
4	EE _x	2	0	1	4	1	2	0	2	0	0	0
6	HM	2	1	0	6	1	3	0	3	1	1	0
1	FF	0	0	0	0	0	0	0	0	0	0	1
6	MOT	0	0	0	5	3	4	3	5	0	2	5
3	ID _r	0	0	0	2	1	0	0	1	0	0	1
1	CD _r	0	0	0	1	1	0	0	0	0	0	0
1	ED _r	0	0	0	0	0	0	0	0	0	0	1
2	Fd _N	0	0	0	2	1	0	0	1	0	0	0
1	Fd _O	0	0	0	0	0	0	0	0	0	0	1
1	IF _d	0	0	0	0	0	0	0	0	0	0	1
1	DR	0	0	0	1	0	0	1	0	0	0	0

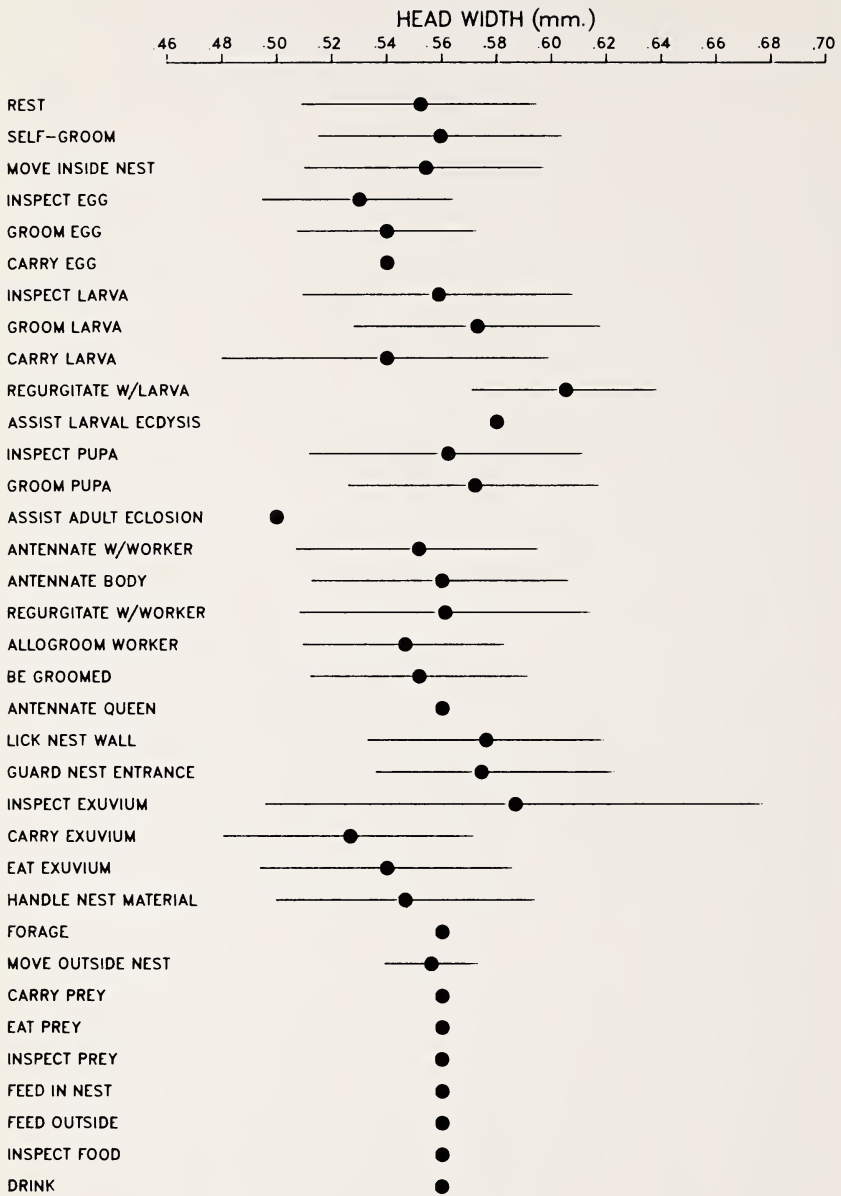


Figure 4. Head width distributions for workers exhibiting behaviors in the ethogram. Means and standard deviations are plotted.

Table 7. Results of ANOVA tests of mean head widths for workers exhibiting different behaviors. Starred entries indicate average head widths were significantly different (LSD tests; * $P < .05$).

	RE	SG	MO	IE	GE	CE	IL	GL	CL	RL
RE										
SG										
MO										
IE		*	*							
GE	*									
CE										
IL	*	*	*		*					
GL		*	*		*					
CL										
RL	*	*	*	*	*		*	*	*	
ALE										
IP					*					*
GP										
AAE										
ATW				*			*			*
ATB				*						*
RW				*			*	*		*
ALW				*						*
BG				*						*
ATQ										
LN					*					*
IE _x										
LOT					*					*
CE _x							*	*		*
EE _x							*	*		*
HM										*
FF										
MOT				*			*			*
ID _r										*
CD _r										*
ED _r										*
FdN										*
FdO										
IFd										
DR										*

to *L. longispinosus* (Herbers and Cunningham 1983); to correct for this different rearing condition comparisons below deleted the prey-handling behaviors reported for *L. ambiguus* (Table 3: IDR, EDR, CDR). In addition, colonies had been matched with respect to worker number in order to eliminate variation correlated with colony size (Table 2). Therefore, comparisons between these studies

were not confounded by variation between observers, husbandry techniques, or colony size.

The two species are ecologically similar. Both inhabit temperate forests throughout eastern North America, nest in small plant cavities such as acorns, twigs, and hollow roots, and scavenge for arthropod parts. On the Huyck Preserve, *L. longispinosus* is more common, preferring deep woods, while *L. ambiguus* appears restricted to relatively open habitats; despite some microhabitat segregation, the two do co-occur in many places.

A subjective analysis of their overall demeanor suggests that *L. ambiguus* is the higher-tempo species (*sensu* Oster and Wilson 1978). That is, they are more excitable and appear to move faster than *L. longispinosus*. While this study was not designed to detect tempo differences, one set of behaviors clearly illustrated it: for the *L. ambiguus* colonies, certain workers were often stationed at the nest entrance. While there, they periodically roused to inspect the entrance, moving a few cm outside the opening before returning to their position. This combination (LOT, MOT) was observed for all 3 colonies (Table 3). By contrast, *L. longispinosus* workers only occasionally positioned themselves near the nest entrance, and the apparent guarding behavior was observed for only one of four colonies watched (Herbers 1982). Thus the more excitable nature of the presumed higher tempo species was evident in the colony ethograms.

Both species displayed a division of labor, with similar patterns of polyethism. Roles of brood care, social organization, and nest maintenance were identified in each. For *L. longispinosus*, though, foragers comprised a unique caste whereas in *L. ambiguus* foragers displayed other provisioning behaviors as well. Moreover, in *L. longispinosus* the division of labor was much tighter: very few instantaneous transitions between roles were observed, most of them between brood care and nest maintenance (Herbers and Cunningham 1983). For *L. ambiguus*, transitions among roles were more frequent (Table 5), although less common than chance expectation. Over 30-min. periods, workers of both species switched roles, but again, role-switching was far more common for *L. ambiguus* than for *L. longispinosus*. Therefore, although specialization occurred in both species, division of labor was considerably tighter for one.

A startling difference between species was the strong morphological bias underlying polyethism in *L. longispinosus* but lacking in *L. ambiguus*. Size differentiation according to task was clear in *L. longispinosus*; the pattern strongly corroborated influences of role and caste delineation from the transition matrix (Herbers and Cunningham 1983). For *L. ambiguus*, however, there were relatively few differences in average worker size among behaviors, and those few significant differences were not correlated with roles inferred from behavior transitions. Perhaps the absence of morphological correlation was due to the fact that the range of worker size was narrower for *L. ambiguus* (Figure 3) than *L. longispinosus* (Herbers and Cunningham 1983); a small size range of workers may have precluded task specialization by size for *L. ambiguus*.

Both species displayed considerable among-colony variation with respect to behavior frequency and time budgets. To ascertain the relative importance of within- and between-species variation, cluster analyses were performed. These techniques involve calculating similarity indices for all possible pairwise comparisons. Then each unit (i.e. colony) is placed in a dendrogram based on its similarity to every other unit. If behavior data reflect phylogeny, then the three *L. ambiguus* colonies should form one cluster while the four *L. longispinosus* form a second. Moreover, one might expect colonies with similar numbers of queens to cluster more closely to each other than colonies with different queen numbers.

The simplest comparisons used the matching coefficient, or number of behaviors shared by two colonies relative to the total number observed over all (Cole 1980). This similarity index utilizes information only on presence or absence of behavior types in the ethogram, thereby ignoring relative frequency. Analysis of matching coefficients yielded the dendrogram of Figure 5. This simplest clustering technique produced the satisfying results that *L. ambiguus* colonies were more closely related to each other than to *L. longispinosus* nests: the three formed a distinct cluster. Moreover, queenright *L. ambiguus* colonies were more similar to each other than to the queenless nest; this result, however, was simply an artifact of the presence of behaviors directed towards queens (ATQ, RQ, ALQ) in queenright but not queenless ethograms. Even so, *L. ambiguus* colonies did cluster as expected. However, the *L. longispinosus* nests did not. Two (LI-A and LI-B) clustered closer to *L. ambiguus* nests

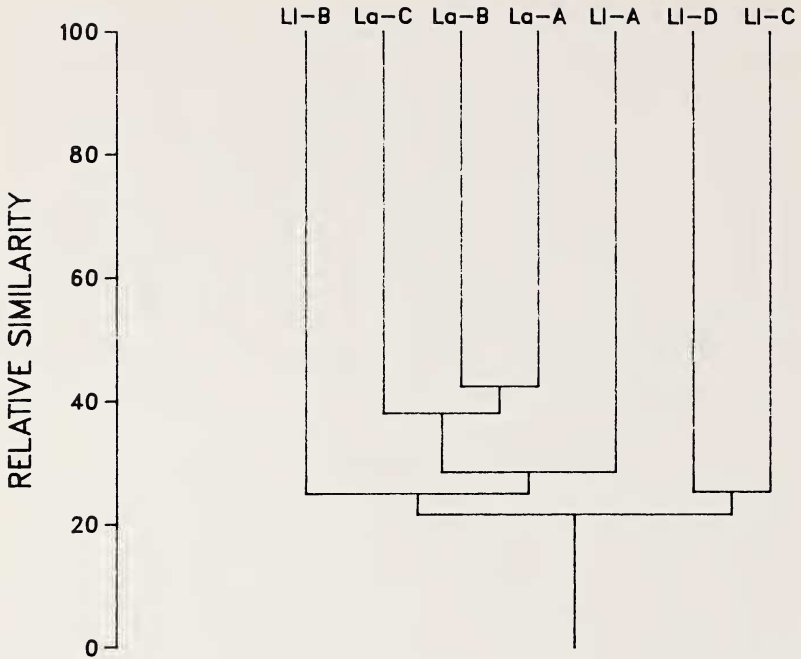


Figure 5. Dendrogram of similarity among *Leptothorax* colonies based on the simple matching coefficient.

than to conspecific nests (Figure 5). The simple matching coefficient which weighs all behaviors equally, therefore produced a dendrogram that gave satisfactory results for one species but far from pleasing results for the second. That is, differences among *L. longispinosus* nests were stronger than differences between species, based on simple matching coefficients.

A second type of cluster analysis used geometric distance between ethogram frequencies of the colonies. This technique incorporated information on frequencies of different behavior types, yielding results more biologically meaningful than the matching coefficient (Cole 1980). For this analysis, rest was excluded. A dendrogram of the seven colonies produced from ethogram frequencies is shown in Figure 6. All colonies were quite similar to each other (minimum similarity was 97.72 on a scale of 100) because proportion data were used. Use of frequencies changes the scale but not relative positions of colonies within the dendrogram. Just as with the simple matching

coefficient, geometric distance between colonies failed to produce separate species clusters (Figure 6). Interestingly, queenright colonies of *L. ambiguus* clustered, as did monogynous colonies of *L. longispinosus*. However, an anomalous cluster was comprised of La-C and LI-D, thereby reducing the significance of other clusters in the dendrogram. In sum, consideration of ethogram frequencies produced a dendrogram for which within-species variation swamped between-species variation.

A final dendrogram was produced from comparison of time budgets over all colonies (Figure 7), based again on geometric distance. This analysis was more discriminating than that based on ethograms (minimum similarity = 83.17). The dendrogram shows three *longispinosus* colonies clustered closely and three *ambiguus* clustered closely. The single aberrant entry was LI-D, a polygynous

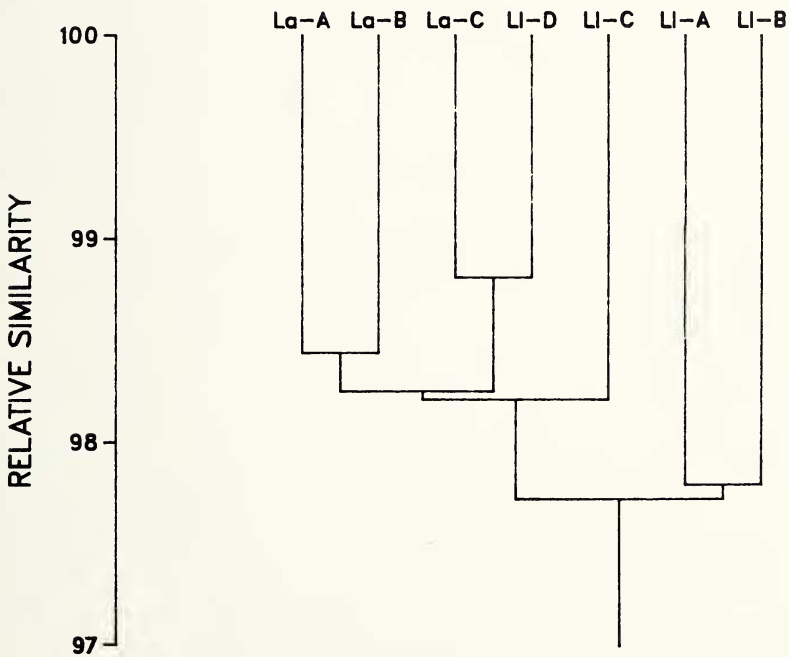


Figure 6. Dendrogram of similarity derived from geometric distance based on ethogram frequencies.

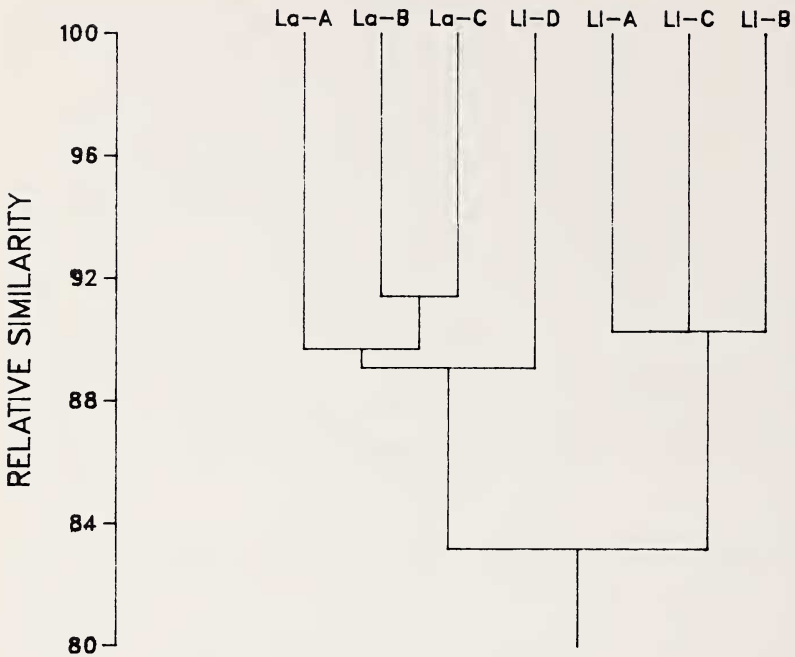


Figure 7. Dendrogram of similarity derived from geometric distance based on time budget frequencies.

longispinosus clustering with the three *L. ambiguus* colonies. Consideration of time budget data gave a reasonable but not perfect fit to expectation.

Of the three dendrograms produced, the best fit to expectation derived from time budget data. Even this best-fit tree, though, contained an anomaly. By no statistical means could I produce a cluster diagram that accorded perfectly to species identity. In no case did the two species separate into discrete clusters. Variation among colonies within a species therefore makes separation between species tenuous. Because most studies report data from a single colony, the utility of cross-species comparisons of behavior is severely limited. Moreover, ethograms themselves appear less discriminating than time budgets for separating out variation between species. It appears, then, that standard methods of reporting social organization (i.e. ethogram frequencies from a single colony) neglect critical information on between-colony variability and on time budgets.